Early Evolution of the Lepidoptera + Trichoptera Lineage: Phylogeny and the Ecological Scenario

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ABSTRACT

New insights in the basal phylogeny of the Lepidoptera shed light on some topical issues in the debate over ecological aspects of the early evolution of this insect "order" and its sister group, the caddisflies. The currently best supported phylogeny of the basal lepidopteran clades is Micropterigidae + (Agathiphagidae + (Heterobathmiidae + (Eriocraniidae + (Acanthopteroctetidae + (Lophocoronidae + (Neopseustidae + (Exoporia + Heteroneura))))))), i.e., it is a richly branched "Hennigian comb". The larvae of Micropterigidae are "soil animals" which feed on foliose liverworts, fungus hyphae and decaying angiosperm material; they live in very moist habitats which probably differed little from those of ancestral Amphiesmenoptera. Exoporian larvae may similarly be broadly classified as "soil animals", and their ancestral life-style was probably very similar to that of micropterigid larvae, except that they lived in silken webbings/galleries. While the exoporian life-style might a priori be considered a retained plesiotypic trait, this interpretation is rejected because splitting events "basad from" the Exoporia + Heteroneura clade repeatedly led to canopy-living clades. It is most parsimonious to consider the ground dwelling of exoporian larvae to represent a secondary habitat shift. The crochet-bearing larval prolegs ascribed to the ground plan of Exoporia + Heteroneura apparently developed in response to a selective pressure for enhancing grips on a silken webbing, rather than for enhancing movement on a smooth plant surface (although the latter role may be the principal one in the bulk of the Lepidoptera). The preferred cladogram necessitates the assumption that an eclosion mode non-dependent on movable pupal mandibles evolved twice in the Lepidoptera: in the Lophocoronidae and in the Exoporia + Heteroneura clade. Larval invasion of genuine aquatic habitats is the key innovation of the trichopteran clade. Problems of recognizing an adult caddisfly as such are briefly discussed; they are particularly serious in the case of fossils. Contrary to the claim of one school of thought on ancestral caddisfly ecology, out-group evidence from the Lepidoptera lends no support to a theory of ancestral caddisflies living in silken tubes. The basalmost lepidopteran clade whose larvae live in silken galleries (the Exoporia) did not arise until the eighth splitting event recognizable among extant forms.

RÉSUMÉ

Les premiers stades de l'évolution dans la lignée des Lepidoptères + Trichoptères : phylogénie et scénario évolutif

Une récente mise au point de la phylogénie basale des Lépidoptères permet d'inférer une nouvelle reconstitution des premiers stades de l'évolution de l'écologie des Lépidoptères et de leur groupe-frère, les Trichoptères. La phylogénie des clades basaux de Lépidoptères la mieux corroborée actuellement est en fait un arbre hennigien « en peigne », arbre abondamment pourvu en rameaux : Micropterigidae + (Agathiphagidae + (Heterobathmiidae + (Eriocraniidae + (Acanthopteroctetidae + (Lophocoronidae + (Neopseustidae + (Exoporia + Heteroneura)))))))). Les larves de Micropterigidae sont des « animaux du sol » qui se nourrissent d'hépatiques, d'hyphes de champignons, et de fragments d'Angiospermes en décomposition ; elles vivent dans des habitats très humides qui diffèrent probablement très peu de ceux des Amphiesmenoptera ancestraux. Les larves d'Exoporiens peuvent être elles aussi considérées grosso modo comme des

« animaux du sol » et leur mode de vie ancestral était probablement très semblable à celui des larves de Microptérigides, à l'exception du fait qu'elles vivaient dans des toiles/galeries de soie. Le mode de vie exoporien pourrait être considéré *a priori* comme la conservation d'un trait plésiotypique, mais cette interprétation est rejetée parce que la cladogenèse des Exoporia + Heteroneura a conduit de manière répétée à l'émergence de groupes vivant dans la canopée. Il est donc plus parcimonieux de considérer la vie au niveau du sol des larves d'exoporiens comme une acquisition secondaire. Les fausse-pattes larvaires munies de crochets, une caractéristique du plan de base des Exoporia + Heteroneura, se sont apparemment développées en réponse à une pression de sélection avec comme fonction l'agrippement sur une toile de soie, plutôt que le déplacement sur les surfaces lisses des végétaux (bien que cette dernière fonction puisse être la plus courante chez les Lépidoptères). Le cladogramme retenu implique qu'un mode d'émergence indépendant de mandibules nymphales mobiles est apparu deux fois chez les Lépidoptères : chez les Lophocoronidae et chez le clade des Exoporia + Heteroneura. La conquête par les larves de véritables habitats aquatiques est l'innovation-clé du clade des Trichoptères. Les problèmes que soulève la caractérisation des Trichoptères adultes sont brièvement discutés ; ils sont particulièrement importants dans le cas des fossiles. Au contraire de ce qui était affirmé par une école de pensée au sujet de l'écologie des ancêtres de Trichoptères, la référence aux Lépidoptères en termes d'extra-groupe n'amène pas d'arguments en faveur de la vie dans des tubes de soie pour les ancêtres des Trichoptères. Chez les Lépidoptères, le plus basal des clades ayant des larves vivant dans des tubes en soie (les Exoporiens) n'est pas apparu avant le huitième événement de cladogenèse identifiable au sein des formes actuelles.

INTRODUCTION

While many (indeed most, KRISTENSEN, 1995) current hypotheses about interrelationships of the higher insect taxa conventionally ranked as "orders" remain inadequately supported, there is very firm support for the monophyly of the entity Amphiesmenoptera, comprising the Trichoptera (caddisflies) and the Lepidoptera. Numerous likely amphiesmenopteran groundplan autapomorphies have been identified in structural traits, and the entity consistently comes out as a monophylum in the molecular analyses I have seen (PASHLEY *et al.*, 1993; WIEGMANN, 1994; REGIER *et al.*, 1995; WHEELER, unpublished).

The Amphiesmenoptera as a whole are one of the most species-rich lineages within the endopterygote insects, hence within the living world, and the Lepidoptera include the largest lineage of primarily herbivorous animals (POWELL *et al.*, in press). Considerable attention has been paid to the patterns of early phylogenetic diversification within the Amphiesmenoptera, and as far as the lepidopteran lineage is concerned a large basal section of the phylogenetic tree now appears fully resolved.

In recent years the application of "tree thinking" to life-history traits has increasingly been taking evolutionary "scenarios" beyond the narrative stage; MILLER & WENZEL (1995), and references cited therein, provide a timely introduction to (entomological aspects of) this exciting field. The present contribution briefly addresses some major questions concerning the ecological scenario of early lepidopteran evolution in the light of recently gained phylogenetic insights. It also addresses some topical issues in the debate over early caddisfly evolution.

THE ANCESTRAL AMPHIESMENOPTERAN

The numerous structural autapomorphies identified in the groundplan of the Amphiesmenoptera are reviewed elsewhere (KRISTENSEN, 1984b; KRISTENSEN & SKALSKI, in press, have a corrected/updated account).

The said apomorphies notwithstanding, the ancestral amphiesmenopteran must be characterized as an overall quite generalized endopterygote insect. Thus it is notable that this ancestor, in the adult stage, must have retained very primitive traits in the mouth apparatus including, *e.g.*, a movable labrum with extrinsic (frontal) retractors, mandibles with tentorial adductors, and a labium with distinct paraglossal lobes. These plesiomorphies are still present in

the basalmost extant Lepidoptera, and nowhere else among panorpoid endopterygotes. The adult ancestral amphiesmenopteran may well have been a spore-/pollen-feeder like two of these basal lepidopteran families (Micropterigidae and Heterobathmiidae). In any case the moths in question (which do not together constitute a monophylum!) have in their preoral cavity some structural specializations (epipharyngeal brushes, spinose infrabuccal pouch) related to their feeding habits, and these specializations show remarkable similarities with those present in some of the (similarly pollen-feeding!) basalmost Hymenoptera (VILHELMSEN, 1996), which presumably are the closest amphiesmenopteran outgroups that take solid food as adults. The suggestion seems straightforward that (as already suggested by MALYSHEV, 1968) adult spore/pollen-feeding was ancestral in a large monophylum comprising the Hymenoptera plus the panorpoid orders (KRISTENSEN, 1984b).

The larvae in the basal lineages of the other panorpoid insects (Mecoptera, Siphonaptera, Diptera) may be broadly characterized as "soil animals" (Fig. 1). It is true that nannochoristid scorpionflies (presumably the sister group of all other Mecoptera, and overall generalized panorpoid insects) have aquatic larvae, but I am firmly of the opinion that this trait is a specialization *sui generis* in the family, rather than a retained plesiotypic condition: the last-instar larva has open spiracles and the last (non-feeding) phase of this instar is spent in the soil outside the stream (PILGRIM, 1972). Similarly, I believe that those dipteran larvae which are aquatic are all secondarily so. The outgroup criterion thus lends support to the notion that also the larvae of ancestral Amphiesmenoptera were soil dwelling, *i.e.*, that this life-style in extant Lepidoptera-Micropterigidae is genuinely plesiotypic.

THE LEPIDOPTERAN LINEAGE

The groundplan autapomorphies of the Lepidoptera are reviewed in the references cited above for the Amphiesmenoptera. Since lepidopteran larvae initially remained in what is believed to have been the environment of their amphiesmenopteran ancestors, it is unsurprising that their (few) groundplan autapomorphies include none one would immediately consider to be potential environmental adaptations. Note, however, that contrary to a widespread belief the ancestral lepidopteran larva probably had a prognathous head, the structure of which may be somehow related to the life in narrow crevices in the soil/periphyton. Prognathism itself is probably plesiomorphic at the basal amphiesmenopteran level (larvae of annulipalpian and "spicipalpian" caddisflies are prognathous, and so are those of Mecoptera-Nannochoristidae), hence at most an exaptation *sensu* GOULD & VRBA (1982). However, the elongation of the pleurostome (which is a specialization characteristic of derived prognathan heads) is a lepidopteran groundplan autapomorphy (KRISTENSEN, 1984a); the presence of this state in the otherwise typically hypognathous head of higher lepidopteran larvae is a morphological anomaly (DENIS & BITSCH, 1973), which apparently is best explicable in terms of phylogenetic constraints.

An outline of basal lepidopteran clades

Principal recent references on the evolution of the basal lepidopteran lineages are: KRISTENSEN (1984b, in press a, b), KRISTENSEN & SKALSKI (in press), DAVIS (1986, 1987),
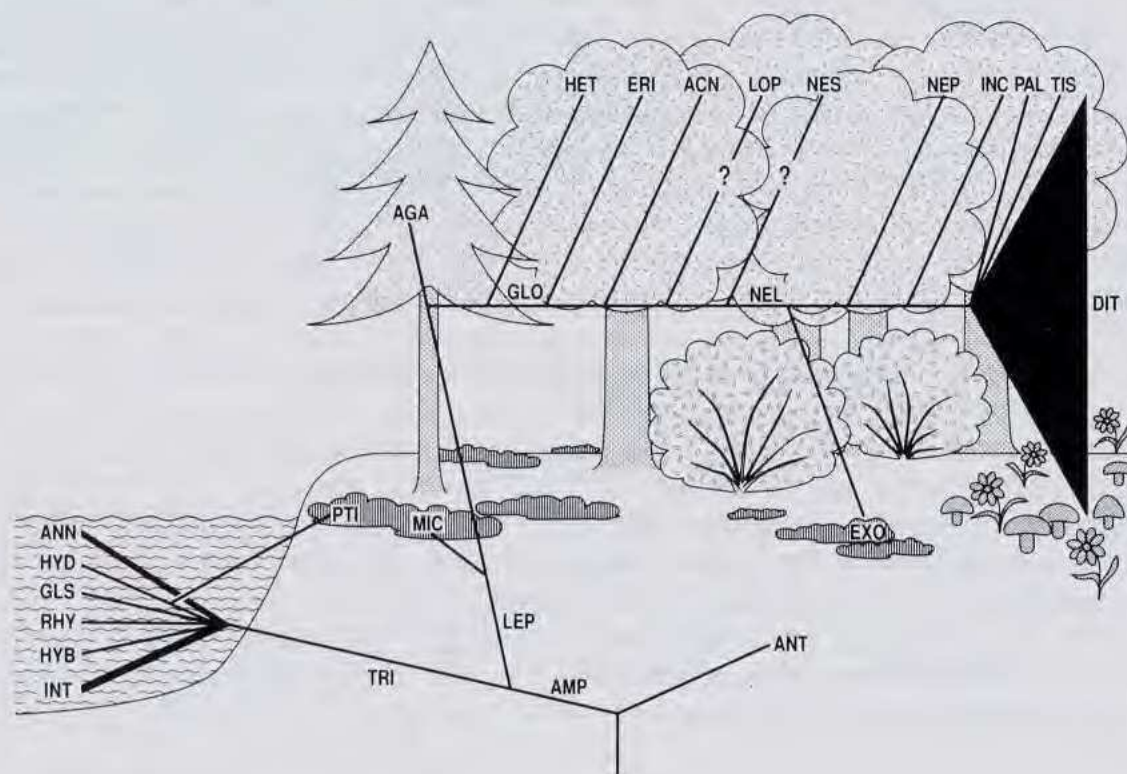
FIG. 1. — Cladogram of basal amphiesmenopteran lineages superimposed on major habitat types; secondary habitat shifts may occur *within* terminal taxa. ACN, Acanthopteroctetidae; AGA, Agathiphagidae; AMP, Amphiesmenoptera; ANN, Annulipalpia; ANT, Antliophora (= Mecoptera + Siphonaptera + Diptera); DIT, Ditrysia; ERI, Eriocraniidae; EXO, Exoporia; GLO, Glossata; GLS, Glossosomatidae; HYB, Hydrobiosidae; HYD, Hydroptilidae-Hydroptilinae; HTB, Heterobathmiidae; INC, Incurvarioidea; INT, Integripalpia; LEP, Lepidoptera; LOP, Lophocoronidae; NEL, Neolepidoptera; NES, Neopseustidae; NEP, Nepticuloidea; PAL, Palaephatidae; PTI, Hydroptilidae-Ptilocolepinae; RHY, Rhyacophilidae; TRI, Trichoptera; TIS, Tischeriidae.

NIELSEN (1989), NIELSEN & KRISTENSEN (1996) and POWELL *et al.* (in press). Problems of formal classification are discussed by KRISTENSEN (*in* CARTER & KRISTENSEN, in press); it is here advocated that recognition of sub- and infraorders in the Lepidoptera should be discontinued.

Four primary lepidopteran clades are currently recognized: the families Micropterigidae, Agathiphagidae and Heterobathmiidae, and the high-rank taxon Glossata comprising all other Lepidoptera, *i.e.*, 99.9% of the described species. SHIELDS (1993) and IVANOV (1994) considered the first splitting event traceable in extant Lepidoptera to have been between the Agathiphagidae and all other clades, but for reasons discussed elsewhere (KRISTENSEN, 1984b, in press a; KRISTENSEN & SKALSKI, in press), I believe the interrelationships should be represented as Micropterigidae + (Agathiphagidae + (Heterobathmiidae + Glossata))(Fig. 1); the latter phylogeny has also received support from analyses of 18S rDNA (WIEGMANN, 1994).

The Glossata comprise six basal clades: the families Eriocraniidae, Acanthopteroctetidae, Lophocoronidae, Neopseustidae, and the high-rank taxa Exoporia (Mnesarchaeoidea + Hepialoidea) and Heteroneura (all remaining Glossata). A recent analysis of the interrelationships of these clades, based on 47 characters in skeletal and "soft" anatomy, has yielded a single most parsimonious solution (Figs 1-2), *viz.*, Eriocraniidae + (Acanthopteroctetidae + (Lophocoronidae + (Neopseustidae + (Exoporia + Heteroneura)))). A suprafamilial taxon "Dacnonypha" comprising the Eriocraniidae, Acanthopteroctetidae and Lophocoronidae is therefore non-monophyletic and must be discarded. A detailed presentation of the analysis, including evidence for the monophyly of each of the six clades, is given by NIELSEN & KRISTENSEN (1996). Names have been given to a selection of the high-rank clades that are recognized: the Exoporia + Heteroneura have long been known as the Neolepidoptera, the Neopseustidae + Neolepidoptera are called Myoglossata, and the name Coelolepida has now been applied (NIELSEN & KRISTENSEN, 1996) to the entity comprising all non-eriocraniid Glossata.

As is well known, the vast majority (>98%) of the extant Lepidoptera pertain to the heteroneuran clade Ditrysia; four other heteroneuran basal clades are recognized, *viz.*, the Nepticuloidea (Nepticulidae + Opostegidae), Incurvarioidea (six families), Palaephatoidea (Palaephatidae only) and Tischerioidea (Tischeriidae only). The interrelationships within the Heteroneura remain unsettled, but the phylogeny represented as Nepticuloidea + (Incurvarioidea + (Palaephatoidea + Tischerioidea + Ditrysia)) may be best supported at present (KRISTENSEN & SKALSKI, in press).

The oldest known fossil moth is *Archeolepis manae* Whalley, 1985 from the Lower Jurassic; its systematic position within the Lepidoptera is unclarified. The fossil record has so far contributed little to the dating of early splitting events within the "order" (*cf.* below), but apparently reliably identified leaf mines of Ditrysia-Gracillariidae (LABANDEIRA *et al.*, 1994) from the Middle Cretaceous (97 myr B.P.) are evidence that all major homoneurous and monotrysian lineages existed by that time.

Life history patterns of non-ditrysian moths

It is unknown whether agathiphagid moths feed at all, but because of the absence of incisivus teeth on their mandibles it is unlikely that they utilize solid foods. In contrast, the adult insects belonging to the two other pre-glossatan families feed on pollen or (in the case of some micropterigids from New Caledonia and [D. LEES, personal communication] Madagascar) fern spores. The stem lineage (*sensu* Ax, 1987) of glossatan moths was characterized by the loss of mandibular function in the post-pharate adult, and the development of the coilable proboscis from the maxillary galeae. Hereby adults of all higher Lepidoptera were rendered dependent on fluid nutrients exclusively.

Larval biologies in the non-glossatan grade are diverse. As noted above, micropterigid larvae are soil dwelling; they feed on foliose liverworts, plant debris and/or fungus hyphae, and they are restricted to quite moist habitats. Agathiphagid larvae are miners in kauri pine (Araucariaceae) seeds; oviposition is believed to take place while the seed is still in the cone, but the larval development and pupation is completed in the seed after it has fallen to the ground. Larval heterobathmiids are leaf miners in *Nothofagus* (Fagaceae), apparently restricted to the deciduous taxa; the fully grown larva vacates the mine, falls to the ground and pupates in a cocoon in the earth.
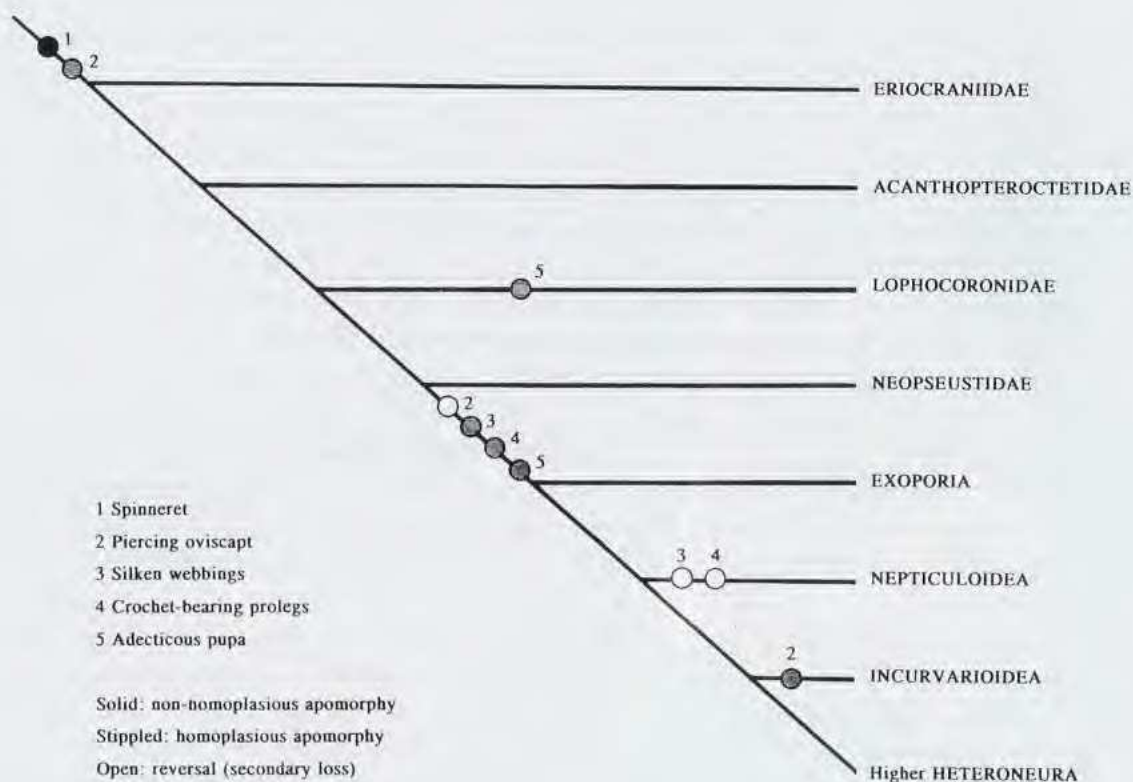
ERIOCRANIIDAE

ACANTHOPTEROCTETIDAE

LOPHOCORONIDAE

NEOPSEUSTIDAE

EXOPORIA

NEPTICULOIDEA

INCURVARIOIDEA

Higher HETERONEURA

1 Spinneret
2 Piercing oviscapt
3 Silken webbings
4 Crochet-bearing prolegs
5 Adecticous pupa

Solid: non-homoplasious apomorphy
Stippled: homoplasious apomorphy
Open: reversal (secondary loss)

FIG. 2. — Cladogram of basal lineages within Lepidoptera-Glossata, with some key evolutionary events indicated.

Among the basal Glossata the Eriocraniidae have a larval biology which is remarkably similar to that of the Heterobathmiidae in the pre-glossatan grade; they are leaf miners, almost exclusively restricted to trees in the Fagales (with a few occurrences on the Rosales), and they pupate in a cocoon in the earth. However, whereas in the Heterobathmiidae the egg is deposited on the host leaf surface (and covered by a secretion) eriocraniid eggs are inserted in pockets in the leaf, cut by the female's piercing oviscapt (Fig. 3). The sole acanthopteroctetid for which the life-history is known is a leaf miner in *Ceanothus* (Rhamnaceae), and it pupates in a cocoon in debris under the host (DAVIS & FRACK, 1987). Immature Lophocoronidae and Neopseustidae are unknown, but since females of the former have a piercing "*Eriocrania*-type oviscapt" (as have the Acanthopteroctetidae), it is believed that their larvae are similarly endophagous, probably leafminers. Neopseustid females also have what appears to be a kind of piercing

postabdomen (clearly distinct from the "*Eriocrania*-type", though perhaps derivable from it), hence immatures in this family may also be endophagous.
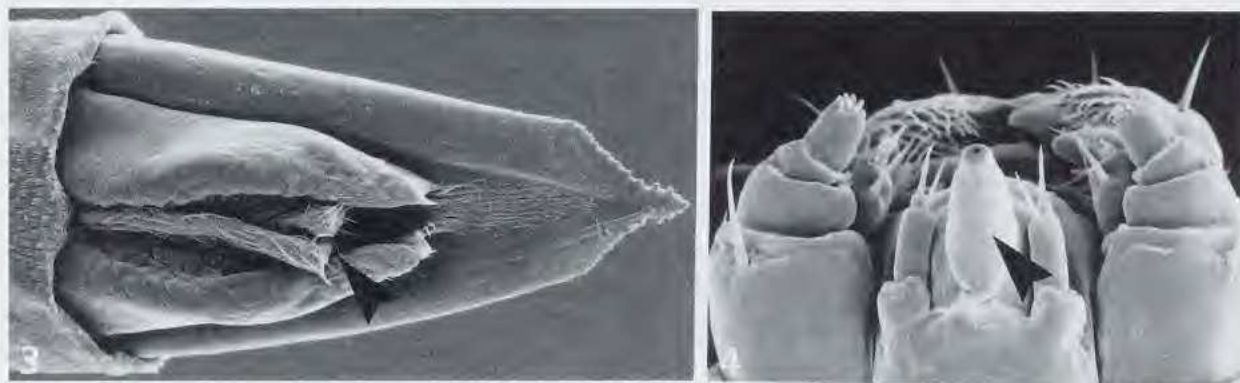
FIGS 3-4. — Eriocraniid structures (SEM), illustrating putative groundplan features of Lepidoptera-Glossata. **3**: *Dyseriocrania subpurpurella* (Haworth, 1828), female abdominal apex (ventral view): "*Eriocrania*-type" piercing oviscapt with lateral "saws"; arrow indicates cloacal opening. **4**: Same, larval mouthparts (ventral view), showing articulated spinneret (arrow).

It is in the Exoporia that one first encounters the "typical lepidopteran caterpillar" with its complement of five pairs of musculated, crochet-bearing prolegs (Figs 6, 7), borne on abdominal segments III-VI and X Mnesarchaeoid larvae are "soil animals" which live in silken tunnels among bryophytes etc, often together with micropterigid larvae, and they are "completely unspecialized phytophages" (GIBBS, 1979). The biology of the "smaller hepialoid families" is poorly known, but larvae of *Ogygioses* (Palaeosetidae) occur in habitats similar to those of mnesarchaeids (DAVIS *et al.*, 1995; HEPPNER *et al.*, 1995). Hepialid larvae (see GREHAN, 1989) have diverse habits. Many make tunnels in the soil or construct silken galleries among litter, feeding on roots or leaves of a variety of plants including pteridophytes, gymnosperms and angiosperms; some are root/stem/branch borers. Fungivory is probably widespread, and a transition from fungivory to phytophagy during larval ontogeny has been recorded in a number of cases.

Most of the known representatives of the smaller heteroneuran lineages feed on living angiosperms, and so did in all probability their last common ancestor. Nepticuloid females deposit their eggs on the surface of the host plant, but all larvae are endophagous: nepticulids mostly leaf-miners, but a few are stem-miners; the few opostegids with known biologies are leaf/petiole- or branch/stem/trunk (cambium)-miners (DAVIS, 1989). The hostplant spectrum of this superfamily, and that of the Incurvaroidea, comprise a large array of (mostly dicot) families. Incurvarioid females have piercing oviscapts somewhat reminiscent of the "*Eriocrania*-type". In the apparently ancestral life-history in the superfamily early larval instars are leaf-mining, while the older instars live on the ground, bearing a portable case constructed from the excised walls of the mine and feeding on living or dead plant material. In some Adelidae even the first-instar larvae are free-living soil-animals, but it is remarkable that these moths also have retained the endophytic oviposition mode. The permanently endophagous (flower/fruit/stem-boring, gall-

making etc) larvae of the cecidosid/prodoxid clade surely exemplify a pattern which is derived within the superfamily. The few known larvae of Palaephatoidea are initially leaf-miners, later living between two leaves (joined by silk along the margins) and feeding on their the inner epidermis and parenchyme cells. (E.S. NIELSEN, pers. com.); the Tischerioidea are consistently leaf miners. In neither of these taxa are the females equipped for endophytic oviposition.

The major question: derivation of angiosperm feeding in basal moth lineages

Accepting the above conclusion that the soil-dwelling, detritophagous larvae of extant Micropterigidae are overall similar to those of ancestral Amphiesmenoptera, it is pertinent to ask how long this larval life style persisted in the sister lineage of the micropterigids. Do such exoporians as mnesarchaeids or palaeosetids spend their larval stage in the same environment as micropterigids because all their lepidopteran ancestors did so? In this case all other homoneurous moth lineages (with known life histories) would have made independent transitions from the soil to arboreal habitats. Or was this transition made in the stem-lineage of Agathiphagidae + (Heterobathmiidae + Glossata), with the soil-dwelling exoporians representing an evolutionary reversal? By the way, Agathiphagid larvae are classified as "arboreal" in acceptance of the aforementioned inference that the eggs are laid while the seed is still in the cone (and perhaps the initial part of the larval life is spent here before the seed falls to the ground). Also, the Exoporia are here regarded as primarily soil-dwelling, and habitat shifts *within* this clade are disregarded in the present context.

With the availability now of a largely resolved phylogeny for the basal moth clades, parsimony speaks clearly in favor of the latter solution (Fig. 1). While it requires only two steps, the former requires at least five transitions from the soil to arboreal habitats, *viz.*, in the stem lineages of Agathiphagidae, Heterobathmiidae, Eriocraniidae, Acanthopteroctetidae and Heteroneura. It almost certainly requires at least a sixth transition also, since although immature Lophocoronidae are unknown, the presence in lophocoronid females of a piercing "*Eriocrania*-type" oviscapt is strong evidence that these insects have endophytic larvae. Even the female postabdomen of the Neopseustidae has a structure which presumably reflects a boring/rasping oviposition mode that would be unexpected if the larvae lived in soil/periphyton interstices.

Judging from the cladogram of extant moths, angiosperm-feeding was first adopted in the stem-lineage of the Heterobathmiidae + Glossata. And if the Agathiphagidae are indeed the sister-group of all other non-micropterigid Lepidoptera, then parsimony would favour the notion that the last common ancestor of these two lineages had canopy-living and -ovipositing moths. The inference is straightforward that the shift has come about through the utilization of arboreal pollen sources by adults of early moths with soil-dwelling larvae; the same kind of ontogenetic habitat shifts are illustrated by some extant micropterigids.

How does the fossil record comply with the notion of angiosperm feeding in extant pre-glossatan moths (*viz.*, heterobathmiids) being primary? A reliable fossil record of eudicot angiosperms (which include the hosts of extant Heterobathmiidae and Eriocraniidae) dates back no futher than the Early Cretaceous (CRANE *et al.*, 1995). ROZEFELDS (1988) interpreted gallery mines in Jurassic pteridophyte leaves from Australia as being due to Heteroneura-Nepticulidae, but the evidence is inadequate (no frass was detectable in the mines) and the identification was discarded by KRISTENSEN & SKALSKI (in press). However, the assignment of one pre-Cretaceous

moth, *viz.*, the Upper Jurassic *Protolepis cuprealata* KOZLOV, 1989 (Fig. 5) to the Glossata is still being upheld by KOZLOV (see KRISTENSEN & SKALSKI, in press, POWELL *et al.*, in press).
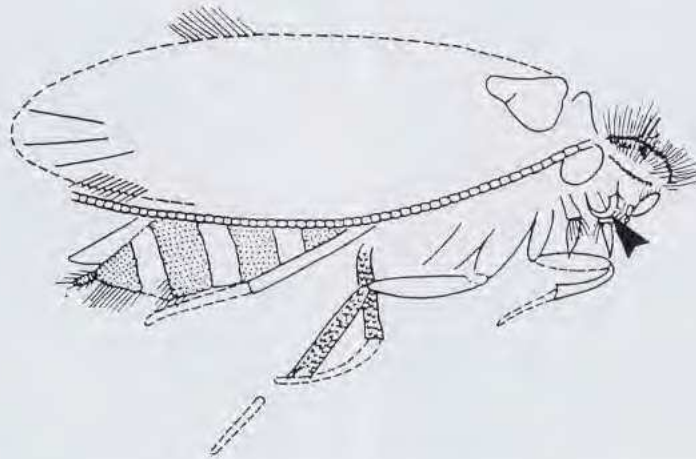

FIG. 5. — *Protolepis cuprealata* Kozlov, 1989; drawning accompanying original description; the arrow indicates the problematical mouth appendage: proboscis or maxillary palp?

Two reservations are in order. Firstly there is, of course, a theoretical possibility that the fossil history of eudicots may be considerably older than documented by fossils, though the counter-evidence presented by CRANE *et al.* is seemingly strong (absence of characteristic eudicot pollen in numerous rich pre-Cretaceous palynofloras from both hemispheres). Secondly, I remain unconvinced about the glossatan nature of *Protolepis*. In particular I consider it likely that the curved mouth appendages are the maxillary palps rather than haustellate galeae; conditions in extant primitive glossatans would lead one to expect the former to be much more prominent formations than the latter. It therefore remains a real possibility that the larva of the last common ancestor of Heterobathmiidae and the Glossata was a leaf miner in a fagacean host, though the possibility of later host switches in the Heterobathmiidae and/or the Eriocraniidae cannot be ruled out. In any case structural modifications linked to the leaf-mining habit has progressed to different stages in these early angiosperm-feeders; for example, eriocraniid larvae have lost the thoracic legs, while these are still retained in heterobathmiids and acanthopteroctetids.

Larval spinning and larval prolegs

Silken threads play a major role in the behavioral diversification of larvae in both amphiesmenopteran "orders". In the first differentiated, "pre-exoporian", lineages of the Lepidoptera, however, the only use made of the larval silk is for the spinning of the cocoon
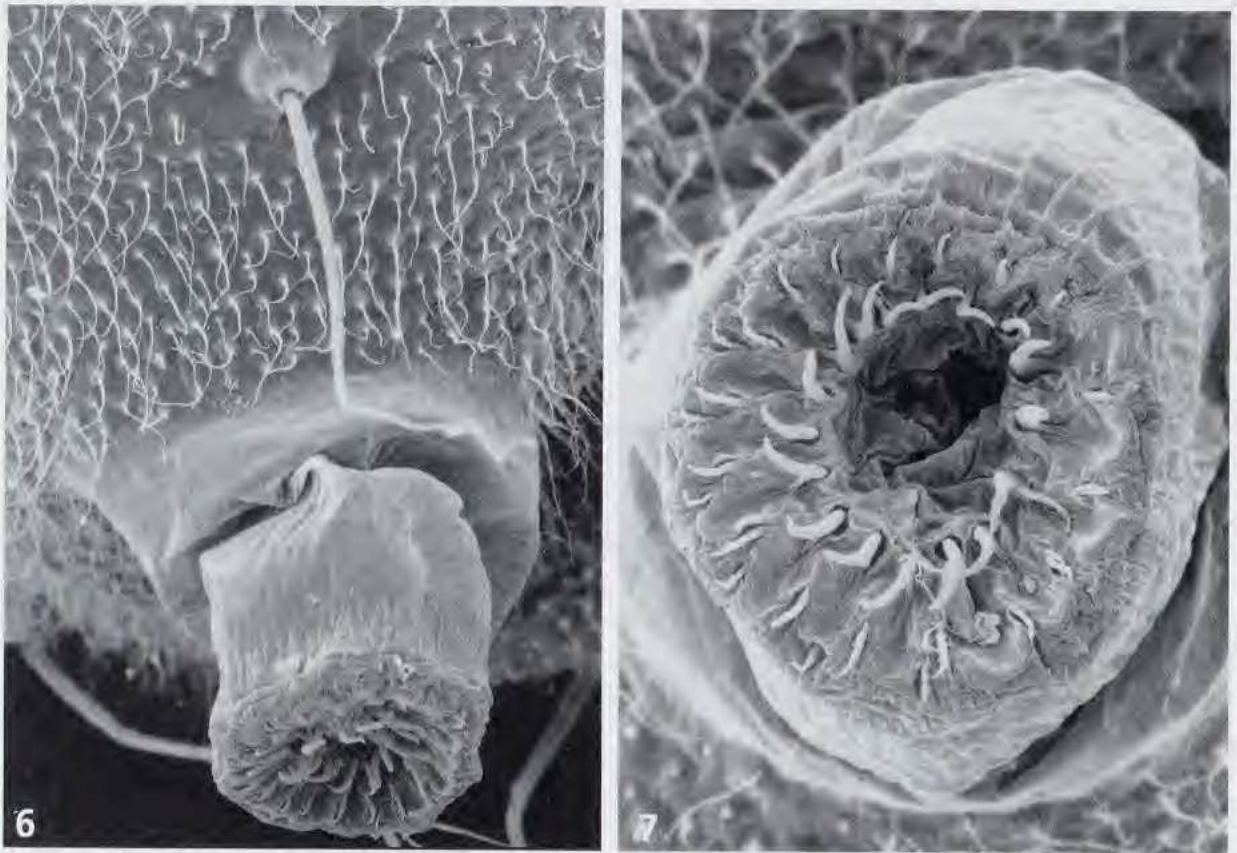
FIGS 6-7. — *Mnesarchaea* sp. (Exoporia-Mnesarchaeidae), crochet-bearing larval prolegs (SEM), illustrating probable neolepidopteran groundplan configuration. 6: Side view. 7: ventral view.

before pupation; such silken cocoons occur in all the known families of this grade (remember that lophocoronid and neopseustid larvae are unknown), Agathiphagidae excepted. Indeed, Agathiphagid pupae remain in the mined seed and have no need for other coverings. However, the labial glands of the larvae are exceedingly large and their secretion presumably plays a major role in the formation of the hard inner lining of the pupal cell. It is perhaps surprising that the development of the "spinneret" (the slender, passively movable process with the spinning gland aperture on the apex, Fig. 4), which is such a prominent groundplan autapomorphy of the Glossata, was not - as far as presently known - initially associated with any marked change in spinning behavior.

The use of silk for construction of galleries or other kinds of webbings in which larvae live is first encountered in the Neolepidoptera. Remarkably, as noted above, it is in the same clade that one first encounters the crochet-bearing proleg (Figs 6, 7) of the "typical caterpillar". It is commonplace to think of these prolegs as an adaptation to clinging to plant surfaces (e.g. STRONG *et al.*, 1984). It must be emphasized, however, that the substrates on which exophagous exoporian larvae move are silk webbings, rather than plant surfaces. Larvae of ancestral Exoporia probably lived in spinnings among periphyton as described above for mnesarchaeids, and as noted by GREHAN (1989) leaf-feeding hepialid caterpillars usually forage in the immediate vicinity of their tunnel/gallery entrances. Prolegs and crochets are absent (secondarily lost,

according to the most widespread view which I endorse) in the endophagous larvae of the Heteroneura-Nepticuloidea. Prolegs are also poorly developed in the Incurvarioidea and Tischerioidea, but more or less distinct crochets are generally retained in both superfamilies; in case-bearing late-instar incurvarioid larvae the crochets engage in a silken lining of the case (SCHELLAUF, 1994), and tischerioids line their blotch mines with silk.

Since silken webs and crochet-bearing prolegs evolved on the same internode on the lepidopteran cladogram (as constructible on the basis of known, extant taxa), this cladogram cannot in itself provide unambiguous evidence that the prolegs evolved as an adaptation to moving on a silken web; however, functional anatomy corroborates this assumption (SCHELLAUF, 1994). The fact that the convex curvature of a caterpillar crochet faces the substrate, and the tip therefore is directed away from the latter in the resting position (*i.e.*, with the plantar muscle uncontracted) is most readily explicable, if the crochet evolved in response to a selective pressure for enhancing grips on a silken webbing. If the initial selective regime had been for enhancing movement on a smooth plant surface, one would rather have expected crochet curvature to have been reversed. The crochet-bearing prolegs are, therefore, apparently an exaptation to clinging onto plant surfaces, which surely is their principal function in the bulk of the Lepidoptera. In many cases the proleg grip is preceded by the larva fastening silken threads on the substrate, and/or the distal proleg configuration is profoundly modified, as in the "Macrolepidoptera-type" proleg.

Eclosion mode

The stem lineage of the Neolepidoptera is characterized by another notable behavioral innovation: the exarate, decticous pupal type is replaced by the adecticous obtect type. Functionally the loss of mobility of the pupal appendages is compensated for by the development, in the neolepidopteran ground plan, of a spinose pupal abdomen which permits the pharate adult to wriggle out of the pupal enclosure prior to pupation.

Though lophocoronid and neopseustid pupae are unknown, examination of the adult structure permits important inferences. Adult neopseustids have well-developed mandibular muscles, and it has therefore been concluded that their pupae are decticous; moreover, it is inferred that they also are exarate, because all known decticous pupal types are so. Adult lophocoronids, on the other hand, have the mandibular musculature completely reduced, and their pupae are thus necessarily adecticous. However, no inference can be made as to whether they are obtect as in the Neolepidoptera, since adecticous exarate pupae are known elsewhere among endopterygotes.

The preferred phylogeny of the Glossata (NIELSEN & KRISTENSEN, 1996) necessitates the postulate that the adecticous pupae in Lophocoronidae and Neolepidoptera are independently evolved. In the analysis the "cost" of making the origin of the adecticous pupa a unique event through switching the Lophocoronidae to the position as sister-group of the Neolepidoptera is three extra steps. Evidently a future discovery of lophocoronid immatures will be significant in this context. If lophocoronid pupae prove to be obtect and spinose like those of neolepidopterans, the support for the second phylogeny would be at least somewhat strengthened.

It should be emphasized, however, that transitions from the decticous to the adecticous pupal type have occurred repeatedly among endopterygote insects, and homoplasy of this trait

within the Lepidoptera is not unexpected. Functionally the transition appears easily explicable: it frees the insect from retaining, up to the adult stage, the investment of precious proteins in the bulky mandibular musculature, which is used only during a very brief phase of the adult insect's life. Thus, the breakdown of the mandibular musculature which has been observed in post-pharate eriocraniids (as in caddisflies), can begin during pupal life, whereby an earlier re-use of components for *e.g.* oocyte growth or genital-duct secretions is made possible.

THE TRICHOPTERAN LINEAGE

The shift of larval habitat from the soil into the genuinely aquatic environment was arguably the key innovation in the early evolution of the caddisfly lineage. The initial step has probably not been a major one in an ecological sense, inasmuch as some "soil" habitats may well be characterized as at least semi-aquatic. However, as far as known, all extant trichopteran larvae share one significant apomorphy which one would immediately interpret as an adaptation to the aquatic life-style: the apneustic tracheal system. Other trichopteran larval groundplan autapomorphies are regressive traits with less obvious functional significance: greatly shortened antennae without any extrinsic musculature, single maxillary endite lobe and very delicate tentorium (the two lastmentioned states are parallelled in all non-micropterigid Lepidoptera).

More or less pronouncedly terrestrial larvae occur in a number of caddisfly lineages (the Palaearctic limnephilid genus *Enoicyla* is perhaps the best known example), but it has not been questioned that these larvae are all secondarily non-aquatic. Importantly, as noted by HINTON (1958), the *Enoicyla* larva is indeed apneustic.

WIGGINS (1984) drew attention to the life-style of micro-caddisflies of the *Ptilocolepus* group as being particularly close to that which might be inferred for the amphiesmenopteran ancestor of the trichopteran lineage. Their larvae are associated with wet liverworts, as are most micropterigid moths in the *Sabatinca*-group of genera, and they "crawl over dripping tiers of these plants, as often out of water as in it". This caddisfly taxon (comprising the W. Palaearctic *Ptilocolepus* and the Amphipacific-Holarctic *Palaeagapetus*) is currently ranked as a subfamily in the Hydroptilidae (MARSHALL, 1979). It remains debatable, however, whether the diagnostic traits it shares with the Hydroptilinae are actually apomorphies. They are: (1) free-living 1st-4th larval instars, with tergal sclerites on thorax and I-VIII; (2) "hypermetamorphic" last (5th) instar larva with swollen abdominal segments and tergal sclerites on all thoracic segments, living in a two-valve case made from leaf fragments. In the light of the uncertainty about the affinities of the *Ptilocolepus*-group it does seem pertinent to ask again whether they could indeed be the sister-group of all other caddisflies, and their larvae therefore primarily semiaquatic. However, even these larvae are apneustic (I have examined serial sections of the thorax and first abdominal segments of larval *Palaeagapetus* without finding any trace of functional spiracles), and thereby conform with the inferred trichopteran groundplan. On this basis the conclusion seems inescapable that ptilocolepine caddises are derived from ancestors with fully aquatic immatures, as hitherto presumed.

## *How does one recognize an adult caddisfly?*

The trichopteran groundplan autapomorphies mentioned above are all in the larval stage. Indeed, and in striking contrast to the Lepidoptera, adult Trichoptera are actually quite difficult

to diagnose as such. This impression is amply supported by an examination of SCHMID's (1989) somewhat detailed reconstruction of the integumental structure of the ancestral caddisfly.

Alleged autapomorphies hitherto identified in the groundplan of adult Trichoptera (KRISTENSEN, 1991/1994) include: (1) prelabio-hypopharyngeal lobe forming large "haustellum" (protrusible/eversible by blood pressure) with intricate system of canals (formed by modified microtrichia) enabling uptake of fluid nutrients; (2) clypeolabral articulation and extrinsic labral muscles absent (parallelism with Mecoptera); (3) true mandibular articulation absent (parallelism with Lepidoptera-Glossata). Not all of these can be upheld, however. The haustellum itself remains a good autapomorphy of adult caddis flies, indeed it is the only at all "strong" one, but the complement of surface canals cannot. These canals were identified in the Integripalpia by CRICHTON (1957), but while this author found all examined non-Integripalpia (Annulipalpia-Polycentropodidae excepted, most likely due to secondary modification) to have a "granulose" surface texture devoid of canals, KLEMM (1966) construed the microtrichia on the *Rhyacophila* haustellum to be aligned in a manner to form canals somewhat comparable to those of the Integripalpia. It is on this basis that I had attributed a canal system to the trichopteran ground plan. However, by subsequent SEM investigation I have discovered that at least the Hydroptilidae (Ptilocolepinae included) and Glossosomatidae have no kind of longitudinal/radial alignment of haustellum microtrichia, hence no canal system. Instead, in these taxa the haustellar microtrichia (which are simple) are arranged along transverse crests (Figs 8-9). Since this arrangement is reminiscent of the spine armature in the infrabuccal pouches on the hypopharyngeal surface in the non-glossatan moths, it most probably represents the ground plan state in the Amphiesmenoptera and hence in the Trichoptera.

It is similarly necessary to discard the obliteration of the "clypeolabral articulation" as a trichopteran autapomorphy: I have now found that a well-developed clypeolabral membrane is actually retained in several members of the Annulipalpia. But all the caddisflies I have sectioned (including representatives of all primary clades, cp. below) are devoid of extrinsic labral muscles; hence the loss of these muscles may well have been a unique event in the trichopteran stem lineage, *i.e.*, it can upheld as an autapomorphy of the group. So can the loss of genuine cranio-mandibular articulations, associated with the absence of mandibular function in post-pharate adult caddisflies.

It is important to emphasize again that none of the autapomorphies hitherto identified in adult caddisflies are easily observable, and in particular that they are unlikely to be of use in the case of fossils. However, attention shall here be drawn to a venational character which deserves scrutiny as a potential aid in diagnosing Trichoptera: the distal course of the forewing CuP. In most Lepidoptera, including all homoneurous lineages, this vein (often quite weak) is almost straight or at most smoothly curved (Figs 10-11). On the other hand, in all extant basal clades within the Trichoptera it is commonplace that the apical part of this vein is abruptly bent towards the wing margin (Figs 13-15); it therefore reaches the margin only a short distance beyond the anal vein (*i.e.*, the apical "stem" of the "double-Y" formed by the fusion of 1A + 2A + 3A), and it frequently even fuses with the latter (Fig. 14). A modification of this pattern is characteristic of the Hydrobiosidae (SCHMID, 1989). In this family (Fig. 15) the portion of CuP beyond the bend again becomes more or less parallel with CuA2, conferring upon CuP an "undulated" configuration; in some cases (*Australochorema* Schmid and *Apsilochorema* Ulmer are pronounced examples) the apicalmost part of CuP is again sharply bent, so a "double
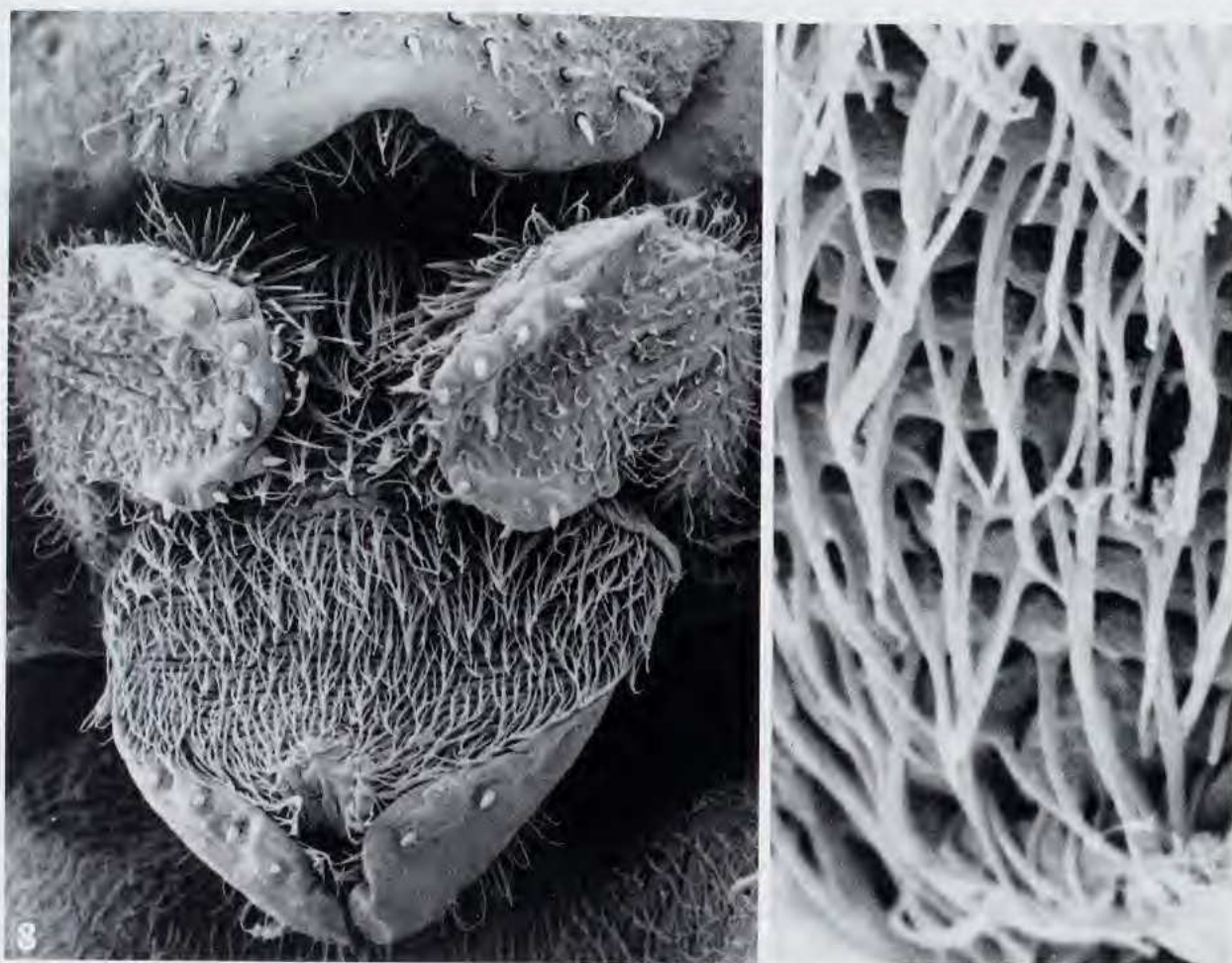
FIGS 8-9. — *Ptilocolepus granulatus* (Pictet, 1834), (Trichoptera: Hydroptilidae-Ptilocolepinae), adult mouthparts (SEM, frontal view). **8**: Haustellum with aligned microtrichia; haustellar base largely covered by maxillary lobes (interpreted as galeae), apex of labrum visible on top. **9**: Microtrichia lines at higher magnification.

undulation" of the vein arises. Most extant and extinct Mecoptera have a straight/smoothly curved CuP, and so do many fossils classified as stem-lineage panorpoids (see WILLMANN, 1989); hence. this state is presumably the plesiomorphic one. But the character is obviously homoplasious (which is unsurprising, given its simplicity). For example, some extant Mecoptera-Bittacidae do have a marked bend, and so do the Permian Amphiesmenoptera-Microptysmatidae, which have a six-branched Rs and therefore presumably can at most belong to the amphiesmenopteran stem-lineage. By the way, WILLMANN (1989) would not exclude that the six-branched Rs could be a microptysmatid autapomorphy. It is also easy enough to find examples of extant caddisflies in which the apical curvature of CuP is little pronounced or even non-existent (Fig. 12), presumably character reversals. The CuP configuration can thus only be taken as an indication of whether a given amphiesmenopteran (extinct or extant) belongs to the trichopteran lineage, not an absolute proof.
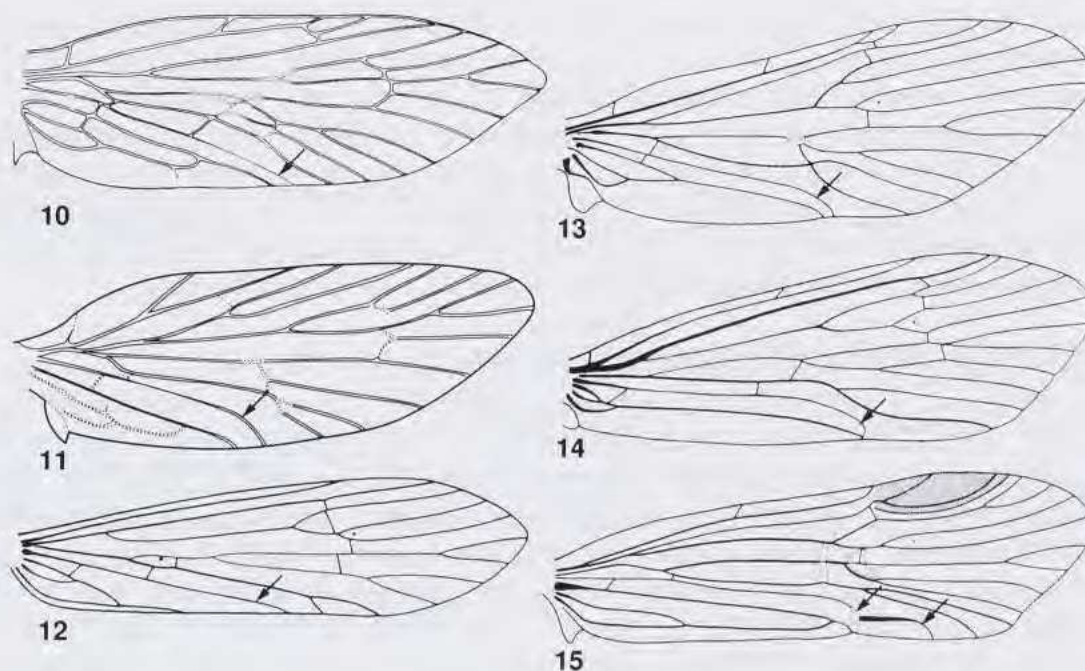
FIGS 10-15. — Forewings of various Amphiesmenoptera (not drawn to scale), illustrating diversity in apical CuP-configuration (arrows). **10:** *Agathiphaga vitiensis* Dumbleton, 1952 (Lepidoptera-Agathiphagidae); note: the pattern of vein branching/anastomosing in the pre-cubital wing area is surprisingly variable from one individual to the next in this taxon. **11:** *Sabatinca calliarcha* Meyrick, 1912 (Lepidoptera-Micropterigidae), exemplifying a primitive moth with unusually strongly bent CuP. **12:** *Psychomyia nomada* Ross, 1938 (Trichoptera-Psychomyidae), a caddisfly with (?secondarily) straight CuP. **13-15:** Caddisflies with CuP strongly bent apically, an auxillary ordinal groundplan autapomorphy: **13:** *Rhyacophila torrentium* Pictet, 1834 (Rhyacophilidae). **14:** *Stenopsychodes tillyardi* Banks, 1939 (Stenopsychidae), showing subapical fusion of bent CuP and fused A veins. **15:** *Australochorema rectispinum* Schmid, 1955 (Hydrobiosidae), showing "double undulation" of CuP. [10-11 original, 12-15 from SCHMID (12: *Mémoires de la Société Entomologique du Canada* **125**, 1983; 13: *Mémoires de la Société Entomologique du Canada* **66**, 1970; 14 : The Canadian Entomologist **101**: 187-224, 1969; 15: *Bulletin de l'Institut Royale des Sciences Naturelles de Belgique*, **59**, Supplement, 1989)]

While NOVOKSHONOV & SUKATCHEVA (1993) opened a recent review by saying that "Caddisflies are common as fossils from the Permian onwards", the earliest concrete evidence for the existence of the trichopteran lineage is actually from the Lower Jurassic, and it is indirect: the existence of the sister-lineage (namely the lepidopteran *Archaeolepis*). I do consider it very likely that the split between the lepidopteran and trichopteran lineages took place at least in the Triassic, but reliable evidence will be difficult to obtain. The assignments of the Protomeropidae, Microptysmatidae, Cladochoristidae, Liassophilidae, Prorhyacophilidae, and Dysoneuridae to the Trichoptera (CARPENTER, 1992; NOVOKSHONOV & SUKATCHEVA, 1993) have all been unfounded within the framework of phylogenetic systematics. Whereas the many costo-subcostal crossveins and/or high number (>4) of Rs branches in the four firstmentioned taxa would seem to

preclude that these can even belong in the amphiesmenopteran "crown-group" (Amphiesmenoptera *sensu* HENNIG), the two lastmentioned may indeed comprise members of the trichopteran lineage; they may, however, equally well include stem-lineage Amphiesmenoptera and stem-lineage Lepidoptera. The same is true of the Necrotauliidae, some Jurassic members of which have the forewing CuP strongly bent apically; these taxa, therefore, can with some justification be talked of as caddisflies. The Upper Jurassic/Lower Cretaceous *Necrotaulius tener* Sukatcheva, 1990 reportedly has a short, annulated apical segment of the maxillary palp; hence it has been assigned to the stem-lineage of the Annulipalpia *s. str.*, and if this palp character is correctly interpreted this assignment is justifiable. It would not be surprising if the extant basal caddisfly clades were indeed differentiated by the Jurassic/Cretaceous boundary.

Basal trichopteran clades and the problems of their interrelationships

Six basal clades are currently recognized within the Trichoptera. The largest are the Integripalpia *s.str.* whose larvae are tube-case makers, and the somewhat less species-rich Annulipalpia *s.str.* (= Curvipalpia) whose larvae are net-spinners/retreat makers. The remaining caddisflies are overall generalized taxa, now grouped into four families: the Rhyacophilidae and Hydrobiosidae (larvae free-living, carnivorous), the Hydroptilidae (larvae free-living, except last instar which make "purse-cases") and the Glossosomatidae (larvae "saddle-case" makers). These four families are believed by some to constitute a monophylum "Spicipalpia" which is the sister group of the Annulipalpia (WEAVER, 1984; WEAVER & MORSE, 1986); alternatively the "spicipalpian" families have been seen as an assemblage which is paraphyletic in terms of the Annulipalpia (SCHMID, 1989), the Integripalpia (ROSS, 1967), or both (cladograms obtained by FRANIA & WIGGINS; WIGGINS, pers. com.). In spite of major recent efforts (FRANIA & WIGGINS, in press) no single convincing phylogeny of the caddisfly clades has so far been obtained.

Considerations of ancestral larval habits/habitats and pupation modes have played a major role in the current debate over these unresolved interrelationships (for an entry into the pertinent literature see WEAVER, 1992a, 1992b; WIGGINS, 1992). In one scenario (WIGGINS & WICHARD, 1989) ancestral caddisfly larvae are believed to have been free-living (at least in earlier instars) and inhabiting cool lotic waters; in another (WEAVER & MORSE, 1986) they are believed to have lived in silken tubes in humus/detrital mats in the lentic or "lotic-depositional" zone.

Both scenarios may well contain elements of the truth. Given the assumption that ancestral Amphiesmenoptera (and indeed panorpoid endopterygots) were soil-dwelling, it is difficult to see how the transition into lotic waters could have taken place via any other habitat than that envisaged in the WEAVER/MORSE theory, though the last common ancestor of the trichopteran crown group apparently, as noted above, has had a more fully aquatic larva than those of extant amphibious spicipalpians like the Hydoptilidae-Ptilocolepinae. On the other hand it must be strongly emphasized, that contrary to WEAVER's claims (1992b), evidence from Lepidoptera lends no support to the notion that trichopteran larvae in silken tubes represent an ancestral amphiesmenopteran life-style. WEAVER referred to the tube-dwelling Exoporia, but since this lineage did not arise until the *eighth* splitting event traceable among extant Lepidoptera, they have little relevance for the question of ground plan conditions in the group, let alone the Amphiesmenoptera. As noted earlier, none of the more basal lepidopteran lineages have larvae that are known to live in silken galleries: out-group evidence therefore supports that the free-living caddisfly larvae represent the ancestral life-style.

Given the long-standing interest in the behavioural diversity of caddisfly larvae, it is much to be hoped that fortcoming renewed efforts will soon result in a trustworthy trichopteran phylogeny upon which this diversity can be mapped and interpreted.

ACKNOWLEDGEMENTS

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